

DIVERSITY OF METAZOAN OVARIES AND
VITELLOGENIC MECHANISMS:
IMPLICATIONS FOR LIFE
HISTORY THEORY¹

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Abstract. — Metazoan life histories are diverse and the selective pressures that have shaped them have resulted in wide interspecific variation in egg size and energy content, fecundity, the age of first reproduction, and the number of and interval between reproductive episodes. Metazoan ovaries show wide morphological variation and a number of mechanisms have evolved by which yolk is synthesized within growing oocytes. The ovary and associated vitellogenic mechanisms play a direct role in the rate of egg production, the frequency of breeding, and the size and energy content of the egg and resultant consequences for larval dispersal. Evolutionary discussions of semelparity vs. iteroparity, r-selected and K-selected species, and the significance of interspecific variability in egg size, energy content and resultant larval mode, should consider the role of oogenesis because the developmental pathways established during oogenesis have a direct effect on subsequent life histories. Reproductive success in both pelagic and benthic marine communities is influenced by a species' capacity to convert food into egg production. The vitellogenic phase of oogenesis is generally the longest phase of egg growth but its duration varies by orders of magnitude between species due to interspecific differences in vitellogenic mechanisms. Metazoans can be viewed on a continuum from slow to fast egg producers, each utilizing physiologically distinct vitellogenic pathways that limit the rate of egg production. Reproductive responses to food vary widely among species and are probably correlated with interspecific differences in digestive kinetics and vitellogenic mechanisms. So-called opportunistic species have evolved specialized vitellogenic pathways for the rapid conversion of food into egg production while many other species (e.g., annual spawners) utilize slower pathways. There exist complex interrelationships between habitat, food, feeding strategies, digestive constraints, and vitellogenic mechanisms that need to be appreciated if marine community dynamics are to be fully comprehended. This review discusses the adaptive significance of metazoan ovaries and vitellogenic mechanisms and their possible life history consequences.

¹ The eighth presentation in the Riser Lecture Series: In 1985 the annual Riser Lecture was initiated by members, alumni and friends of Northeastern University's Marine Science Center, at Nahant, Massachusetts. The occasion was the official retirement of Professor Nathan W. Riser. As teacher, biologist and founder of the facility, "Pete" Riser endowed the laboratory with a legacy, that being the importance of considering one's special focus within the context of the whole organism. The Riser Lecture is dedicated to that principle.

“Though some of the very essential features of oogenesis, such as cytology of maturation divisions, have remained almost the same throughout the animal kingdom, differences exist among various groups in details of structure, chemistry, and physiology of the female gamete and its spawning behavior; others are directly traceable to varied demands imposed by the habitat and life cycle (Adiyodi & Adiyodi 1983).”

One goal for undertaking life history studies is to predict what kind of life history pattern an organism will display in any given habitat. Such a predictive ability should lead to a better understanding of the selective forces that shape the evolution of life histories and produce the diversity of patterns observed in nature. The reproductive biology of any species represents a collection of traits that have been subject to selection and presumably represent adaptive features (Gould 1977, Raff & Kaufman 1983, Ghiselan 1978). Many of these reproductive traits act as covariables and often evolve in concert. To determine a species' “fitness” and to better understand marine community structure, life history theorists have tried to understand the evolution and ecological significance of numerous reproductive traits including the number, size, and quality of offspring, the age distribution of reproductive effort, the interaction between reproductive effort and adult mortality, the timing of reproduction, and the variability of these traits among the offspring (Cole 1954, MacArthur & Wilson 1967, Pianka 1970, Stearns 1976).

The consequences of metazoan life history variations for population dynamics were first explored by Cole (1954) and, since then, many clusters of life history traits have been analyzed (Levin & Haggert 1990). Life history theorists generally study population regulation and marine community structure from the point of view of dispersal, predator-prey interactions, and competitive coexistence (Levin 1984). However, many life history traits are constrained by ovarian structure and by species-specific vitellogenic mechanisms that determine the quantity,

quality, and rate of energy (yolk) incorporation into the egg during oogenesis. The rate of egg production, the frequency of breeding, the size and energy content of the egg, and the resultant consequences for larval dispersal (e.g., planktotrophy vs. lecithotrophy), are strongly influenced by the ovary. For successful reproduction to occur, maternal mobilization, biosynthesis and bioaccumulation of nutrients must occur within the egg in a programmed manner during oogenesis. The impact that ovarian evolution has had on metazoan reproductive success is exemplified dramatically by arthropods, which account for more than 90% of the total number of species on earth. A major reason for their success has been the evolution of specialized ovaries and vitellogenic mechanisms that enable them to manufacture, sometimes in a single day, an egg mass exceeding half their body weight (Yamashita & Indrasith 1988). However, many other species have far less capacity for rapid egg production due to constraints that impose limits on the vitellogenic phase of oogenesis. Thus, the length of oogenesis may vary by orders of magnitude from one species to another depending upon the mechanism of vitellogenesis employed during the yolk acquisition phase of oogenesis.

Larval ecologists and life history theorists have focused special attention on the invertebrate egg and the contrast between species that undergo a single reproductive episode during their lifetime (semelparous species) and those that undergo multiple reproductive episodes (iteroparous species). Variability of egg dimensions, energy content, and subsequent larval developmental mode (e.g., lecithotrophy vs. planktotrophy) have evolutionary significance and influence the distribution and abundance of marine species (see Young 1990). Even though yolk is believed to play a pivotal role in larval nutrition and has been the subject of many theoretical discussions (Emler et al. 1987), oogenesis has rarely been considered. To understand the relationship between

ovarian structure and function, energy investment per egg, and larval biology, one must consider oogenesis because interspecific variations in yolk content are established during the vitellogenic phase of egg ontogeny.

Studies of semelparity vs. iteroparity generally focus attention on the spawning event while the period of egg maturation and vitellogenesis, which may have preceded it by weeks or months, is less appreciated. Although many ecologists may be unaware of the diversity of metazoan vitellogenic mechanisms, they are acutely aware of the ecological implications of these mechanisms. For example, species differ in their ability to rapidly respond to open, unexploited, or organically enriched habitats. Species that do respond rapidly have been labeled "opportunistic" (MacArthur 1960, Hutchinson 1967) or "r-selected" (MacArthur & Wilson 1967). Species with opportunistic life histories mature early and undergo frequent reproductive episodes, enabling them or their offspring to adapt through short-term selection (Grassle & Grassle 1974). For egg production to proceed at an accelerated rate, the egg must incorporate nutrients quickly. For other species, however, oogenesis is often an annual event, requiring months of egg maturation resulting in a relatively predictable seasonal reproductive episode. Such slow egg production is usually preceded by a programmed energy transfer from somatic storage sites to the ovaries as exemplified by most echinoderms (Pearse & Cameron 1991). Semelparity and iteroparity, therefore, represent life history manifestations of different vitellogenic mechanisms, some of which are adapted for the rapid synthesis of yolk, while others are not (Eckelbarger 1983). In recent years, comparative studies of oogenesis have revealed a correlation between life histories and patterns of oogenesis in cnidarians (Eckelbarger & Larson 1988, 1992; Eckelbarger 1994), ctenophores (Greve 1970), polychaetes (Eckelbarger

1983), oligochaetes (Jamieson 1991), nematodes (Stark 1984), rotifers (Bentfield 1971), ectoprocts (Reed 1988, 1991), insects (Davidson 1986), and crustaceans (Blades-Eckelbarger, pers. comm.). Therefore, developmental pathways established during oogenesis have a direct effect on subsequent life histories.

A number of excellent reviews on oogenesis are available but most have targeted specific events of cell differentiation and the processes that regulate developmental pathways (see Wourms 1987, for review). Few investigations have addressed the ecological significance oogenesis has played in life history evolution. This review will examine the diversity of metazoan ovaries and vitellogenic mechanisms and assess their possible life history consequences.

Invertebrate Ovaries and Accessory Cells

Invertebrate ovaries range from loose associations of germ cells to morphologically complex organs. Two types of oogenesis have evolved in the invertebrates (Eckelbarger 1983). *Extraovarian* oogenesis involves the release of oocytes from the ovary early in their development (often before vitellogenesis begins) and the subsequent completion of development elsewhere, frequently within a coelomic space (e.g., polychaetes). *Intraovarian* oogenesis, the more common pattern, involves the retention of oocytes in the ovary until late in development or just prior to spawning (e.g., echinoderms and molluscs). In either case, oocytes may or may not be associated with accessory cells during oogenesis. The majority of invertebrates possesses distinct (localized) ovaries in which the oocytes are closely associated with accessory cells that fall into one of four general categories: 1) follicle cells, 2) nurse cells, 3) nutritive eggs, or 4) other miscellaneous accessory cells (Wourms 1987). Accessory cells are commonly assumed to play a trophic role but supportive evidence is usually lacking. Al-

though the topographic, structural, and functional interrelationships between germ cells and accessory cells are poorly understood in most species, numerous examples are available that demonstrate that some ovarian accessory cells may have ecological significance because they enable the organism to accelerate egg production through trophic support of the growing oocyte.

Follicle cells are somatic in origin (non-germ cell line) and partially or completely encompass individual oocytes or groups of oocytes. They are believed to have at least four distinct functions: 1) mechanical support or protection of oocytes during early oogenesis, 2) the production of secondary, compound, or cellular egg envelopes around oocytes, 3) the synthesis of metabolites or yolk precursors, and/or 4) the resorption of atretic oocytes (Wourms 1987). Nurse cells are abortive germ cells that are associated with oocytes through confluent cytoplasmic bridges resulting from incomplete cytokinesis (Huebner & Anderson 1976). They have been reported from many invertebrate phyla. In general, nurse cells replace or supplement the biosynthetic activities of the oocyte. They may have a trophic function by contributing organelles (i.e., mitochondria), ribonucleoproteins, and/or pre-yolk or fully formed yolk bodies to the oocyte, or they may play a role in determining oocyte polarity (Wourms 1987). Nurse cell-oocyte complexes are most highly developed in insects. The more primitive species possess panoistic ovaries that contain only follicle cells while the higher insects have meroistic ovaries with well-developed nurse cell-follicle cell complexes that contribute significantly to oocyte development (Telfer 1975).

In some species (e.g., sponges, hydroids, some polychaetes, and *Artemia*), a few germ cells abort their development and are phagocytized as "nurse eggs" by one or more oocytes. Neophoran turbellarians are unique because yolk is not synthesized in the egg but rather in special accessory cells

(vitellocytes) that are deposited within the alecithal eggs and later engulfed by developing embryos (Gremigni & Falleni 1991). Therefore, the egg acquires yolk during embryonic development rather than during oogenesis. Prosobranch gastropods, particularly the neogastropods, show additional examples of post-oogenic yolk transfer in that non-viable, nutritive eggs are deposited within egg capsules to serve as supplemental sources of nutrition for the developing embryos (Rivest 1983).

In echinoids, large vesicular cells called nutritive phagocytes appear to sequester nutrients prior to vitellogenesis and transfer them via a diffusional process to the oocytes (Pearse & Cameron 1991). A number of recent studies on echinoids has also implicated the intestine, ovary and coelomocytes as sites of yolk protein synthesis but these results warrant further investigation (reviewed in Pearse & Cameron 1991). Among anthozoans, specialized gastrodermal cells collectively referred to as the trophonema, become intimately associated with developing oocytes and are believed to play a nutritional role by mediating the movement of yolk precursors from the coelenteron to the egg (Fautin & Mariscal 1991). Within the Scyphozoa, specialized gastrodermal cells termed trophocytes serve a nutritive role during oogenesis in a manner similar to that described in anthozoans (Eckelbarger & Larson 1988, 1992; Eckelbarger 1994). Figure 1 summarizes the potential sources of yolk precursors available to metazoan oocytes during vitellogenesis.

Phyletic Constraints on Vitellogenesis

Organisms display a variety of life history traits that can be correlated with unique morphological constraints determined by ancestry. To understand the significance of diversity in metazoan ovaries and vitellogenic mechanisms, one must first consider the bewildering variety of architectural themes observed in the Metazoa. Although



Fig. 1. Sources and routes of yolk precursor entry into developing oocytes in different metazoans. 1) low molecular weight precursors enter oocyte through surface microvilli; 2) large molecular weight yolk precursors enter oocyte via receptor-mediated endocytosis; 3) yolk precursors derived from coelomic eleocytes enter oocyte via endocytotic uptake; 4) follicle cell-derived yolk precursors enter oocyte via endocytotic uptake; 5) nurse cells provide metabolites and/or organelles to oocyte via intercellular bridges; 6) both follicle cells and nurse cells are involved in support of oocyte growth; 7) oocyte phagocytizes germ or somatic cells during growth phase; 8) blood vessel-derived precursors are incorporated into oocyte via endocytic uptake.

all oocytes require an external source of energy for yolk synthesis, the options for acquiring yolk precursors are constrained by the body plan of the organism in which they reside. For example, lower metazoans (e.g., placozoans, sponges, cnidarians, small-bodied, interstitial species) are structurally simple, lack well-developed circulatory systems, fluid-filled body cavities and complex ovaries that could provide nutritional support to the growing oocyte. They also have

fewer and less specialized cell types so oocytes often grow autonomously without the aid of accessory cells. Germ cells in the sponges and cnidarians are often motile and capable of actively migrating toward their own sources of nutrition. Simple diffusion or active transport of precursors to the oocytes from digestive cells may be adequate to support oocyte growth in many small-bodied infaunal organisms particularly since few eggs are produced at one time. The di-

rect transport of dissolved organic materials (DOM) from the external environment through the body wall also may play a role in oocyte nutrition (Manahan et al. 1982). In contrast, species in the higher phyla (e.g., vertebrates) deliver yolk precursors from extraovarian sources via the circulatory system to a static oocyte growing within a relatively complex ovary.

Oocytes often depend to some extent on the trophic support of cells and tissues that are spatially close to the ovary or can communicate with the ovary via the circulatory system or adjacent fluid-filled cavities. Therefore, similar mechanisms of oocyte nutrition have arisen independently in different taxa when there are structural similarities in their body plans. Nurse cells, for example, play some role in support of oocyte growth in many species and may have arisen independently within many phyla because early germ cells initially undergo mitotic division within the ovary. In most instances, the cytoplasmic continuity between sibling germ cells is lost and each cell develops into an independent, viable egg. In other cases, intercellular bridges remain intact and some germ cells are restricted to only a trophic role. The extent of nurse cell involvement in oocyte nutritional support is significant in ctenophores, rotifers, and insects. Follicle cells are perhaps the most ubiquitous ovarian accessory cell. They are particularly common among coelomates because they are derived from the peritoneum which is intimately associated with the ovary. In some annelids, molluscs, crustaceans, insects and ectoprocts, the follicle cells often undergo hypertrophy prior to or during vitellogenesis and contain abundant proteosynthetic organelles that are probably involved in yolk precursor production.

It is likely that yolk precursors often pass directly or indirectly from the digestive system to developing oocytes, particularly in small-bodied species that produce only a few eggs at a time. The intimate association

of oocytes with digestive systems is a common theme in cnidarians, nemerteans, and molluscs, for example and this method of nutrient acquisition has been proposed for gastrotrichs (Rieger & Rieger 1980) and interstitial polychaetes (Eckelbarger 1983). Stricker (1986) suggested that yolk precursors originating from the gut may be passed to the ovary through intervening accessory cells in the ectosymbiotic nemertean *Carcinonemertes epialti*, a species that rapidly produces eggs while feeding on the eggs of host crabs. In nematodes, yolk proteins are produced by the gut and transferred through the pseudocoel to the ovary allowing some species to be among the most fecund on earth (Kimble & Sharrock 1983). In some species, close apposition of oocytes to the digestive system may be adequate for the transfer of nutrients during oocyte growth (e.g., polychaetes and coronate scyphozoans) while in other species, specific digestive cells have assumed a trophic role (e.g., anthozoans and semaeostome and rhizostome scyphozoans). In vertebrates, the circulatory system is an efficient means of transferring vitellogenin to the oocytes. In some invertebrates, notably the polychaetes and cephalopod molluscs, the circulatory system is also used to transfer yolk precursors to the ovary. The funicular system in bryozoans has been cited as a possible means of precursor transport to the ovaries of individual polypides, analogous to that observed in polychaetes (Reed 1988). Many invertebrates have fluid-filled cavities surrounding the ovaries that enable precursors to be transferred to developing oocytes from their extraovarian sites of production. Thus the hemocoels of crustaceans and bivalve and opisthobranch molluscs, the pseudocoel of nematodes, the coelom of annelids, and the perivisceral coelom of echinoderms all serve potentially as reservoirs for precursor storage and a means of inter-organ nutrient transfer to the oocytes from the extraovarian site of precursor synthesis. These

cavities also permit the accumulation and storage of large numbers of eggs prior to spawning.

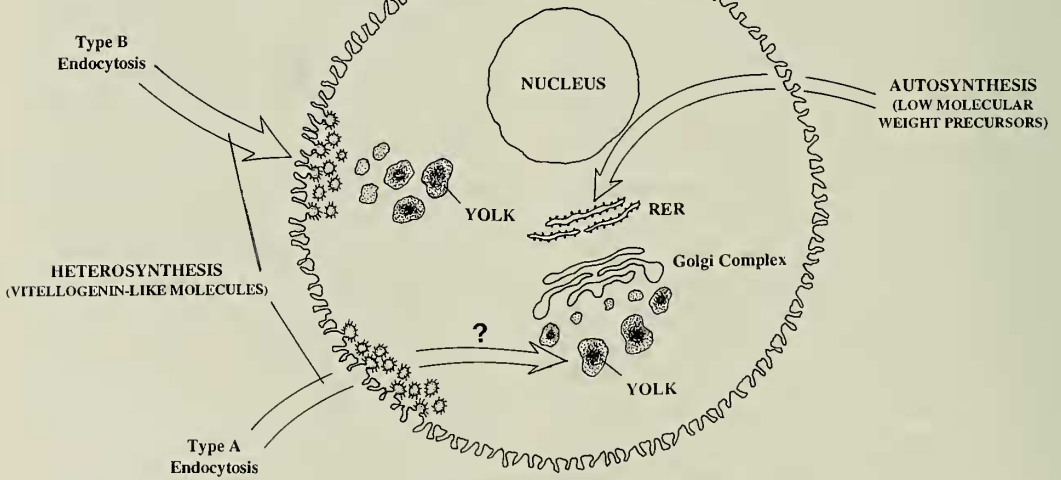
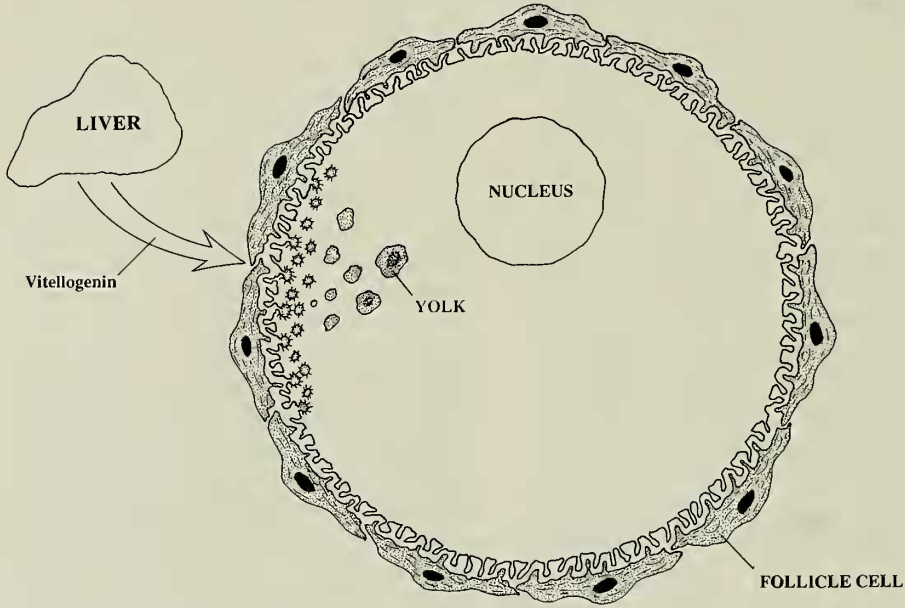
Mechanisms of Yolk Synthesis (Vitellogenesis)

The egg cell is typically the largest cell within an organism due to incorporation of substantial quantities of ooplasmic energy reserves collectively called "yolk." The biosynthesis and accumulation of yolk represents a substantial energy investment by the female and is a complex and highly regulated process under both genetic and endocrine control. Vitellogenesis is usually the longest period of oocyte differentiation but it varies in length by orders of magnitude from one species to another. The rate of yolk synthesis is dependent on the capacity of the oocyte or other mediating cells to obtain and convert yolk precursors into yolk bodies. That, in turn, is dependent on the structure of the ovary and the mechanism(s) of vitellogenesis that characterize each species. Due, in part, to morphological constraints imposed by ancestry, members of different phyla often utilize different vitellogenic mechanisms. This vitellogenic diversity has resulted in profound implications for their subsequent life histories by limiting the maximum rate of egg production and the interval between egg-laying events. In its broadest sense, yolk includes a heterogeneous population of ooplasmic inclusions including lipid droplets, glycogen granules, and chemically complex, membrane-bounded organelles containing proteins, carbohydrates, lipids, pigments, free amino acids, free sugars, nucleotides, and nucleic acids. Wourms (1987) outlined the types of carbohydrate, lipid, and protein components of yolk that are encountered in most eggs. Carbohydrate yolk reserves include glycogen, galactogen and various polysaccharide-protein complexes. Lipid reserves include "fatty" yolk globules, phospholip-

ids, and triglycerides. Protein reserves include "protein yolk" consisting of chemically uncharacterized protein reserves, lipoproteins, phosphoproteins (vitellogenins), and protein-polysaccharide complexes. Although individual authors often neglect to define their use of the term "yolk," they are usually referring to characteristic, electron dense organelles (yolk granules) that dominate the ooplasm of the mature egg and distinguish the egg from other cells.

Despite myriad papers on vitellogenesis, yolk is one of the least understood components of the metazoan oocyte. Many biologists assume that yolk functions solely as an energy reserve despite scanty supporting evidence. Yolk (vitellin) is ultimately derived from the products of digestion but yolk precursors can be delivered to the oocyte in several forms including low molecular weight precursors, high molecular weight female-specific yolk proteins (vitellogenin), or both. Schechtman (1955) described three mechanisms of yolk synthesis (Fig. 2): 1) autogenous yolk formation occurs when the oocyte synthesizes vitellin using its own proteosynthetic organelles after internalizing low molecular weight, exogenous precursors; 2) heterogenous yolk synthesis occurs when yolk proteins are synthesized by other cells and transported to the oocyte for incorporation; and 3) mixed yolk synthesis in which a combination of autogenous and heterogenous mechanisms are used. In oocytes utilizing heterogenous pathways, a specific class of female-specific yolk proteins referred to as vitellogenin, is incorporated into the oocyte (Fig. 2A) and usually comprises 60–90% of the soluble yolk proteins (vitellins) in the cell (Hagedorn & Kunkel 1979). Vitellogenin is a generic term first applied to female-specific proteins in insects but it has been widely used in vertebrates, and more recently in other invertebrates. Thus far, there is little evidence that vertebrate vitellogenins have more than an analogous relationship to in-

A. VERTEBRATE OOCYTE



B. INVERTEBRATE OOCYTE

Fig. 2. Diagrammatic representations showing pathways of yolk precursor incorporation by nonmammalian vertebrate (A) and invertebrate (B) oocytes.

vertebrate vitellogenin. Yolk inclusions have not been observed in the eggs of mammals, suggesting that the vitellogenin genes were either lost or silenced in the transition from prototherian to therian mammals (Wallace 1985). In general, one observes a progres-

sive adaption of heterosynthetic mechanisms of yolk synthesis as one moves from the lower to the higher phyla, culminating in the non-mammalian vertebrates which employ heterosynthesis exclusively (Fig. 3).

The most common means for determin-

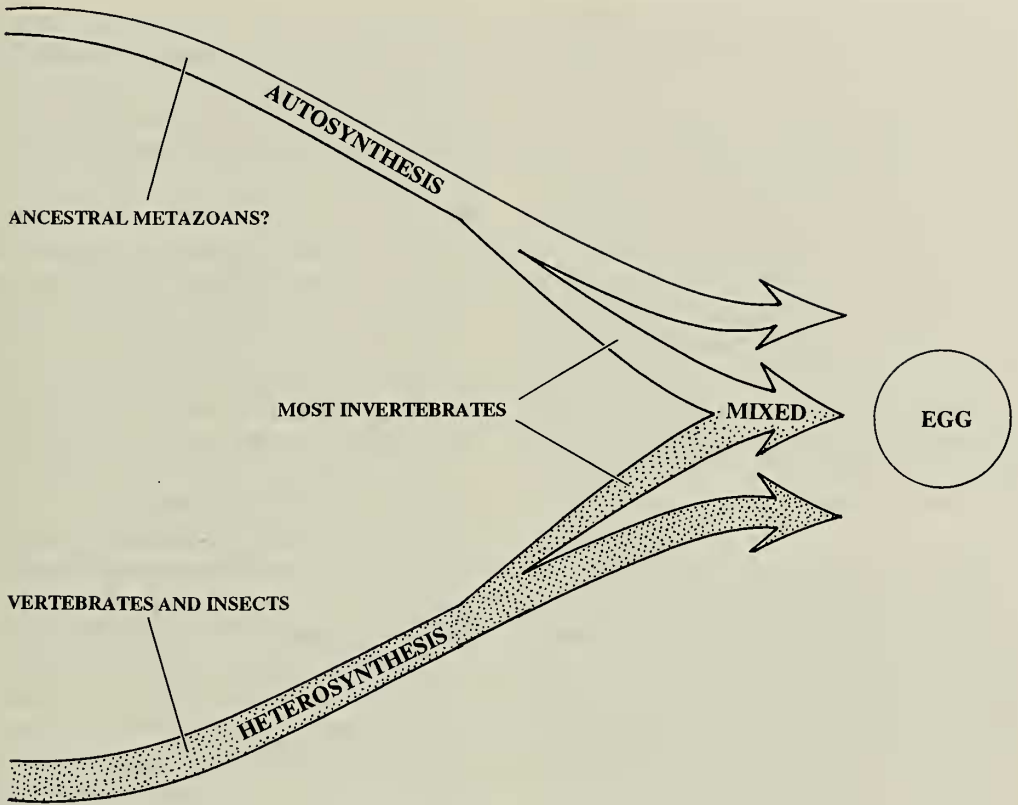


Fig. 3. Hypothetical pathways of metazoan yolk synthesis.

ing the mechanism(s) of vitellogenesis is through inference from ultrastructural observations. Species that utilize autosynthetic mechanisms typically have oocytes containing abundant rough endoplasmic reticulum (RER) and Golgi complexes which appear to collaborate in the biosynthesis of yolk protein(s). In these organisms, there is little or no morphological evidence for the incorporation from extraoocytic sources of large molecular weight yolk precursors by the oocyte and oocyte growth tends to be very slow (Fig. 2B). However, low molecular weight precursors are assumed to be sequestered through the numerous microvilli that typically adorn the oocyte surface. In other species, the uptake of large molecular weight exogenous precursors (vitellogenin?) can be visualized ultrastructurally by the appearance of distinctive coated pits and vesicles (endosomes) along the oocyte sur-

face involving a process of receptor-mediated endocytosis (Fig. 2B) (Wild 1980). High levels of endocytotic activity during vitellogenesis are generally associated with rapidly growing oocytes. In some instances, ultrastructural studies suggest the fusion of endosomes with the products of the RER and Golgi complexes (type A endocytosis). In others, endosomes fuse directly into yolk bodies (type B endocytosis) (Fig. 2B). An assumption is frequently made that ultrastructural evidence of endocytotic activity is sufficient to indicate the incorporation of vitellogenin for yolk assembly. However, the mere presence of coated pits and vesicles does not indicate conclusively that extraoocytic molecules contribute to yolk synthesis unless ultrastructural studies indicate that type B endocytosis results in the direct fusion of endosomes into yolk bodies. Conversely, the absence of endocytotic activity

does not necessarily preclude the possibility of incorporation of heterosynthetic precursors if uptake of high molecular weight precursors is a slow process. For example, nereid polychaetes were considered typical examples of autotrophic eggs due to the presence of abundant RER and Golgi complexes and low levels of endocytotic activity. However, immunological approaches have demonstrated that vitellogenin is actually synthesized by free-floating coelomocytes in *Nereis virens* and *Perinereis cultrifera* and incorporated slowly into the oocytes from the coelomic fluid (reviewed in Fischer & Dhainaut 1985).

Egg Volume and Energy Content

Larval ecologists have drawn attention to the relationship between egg size, energy content (parental investment), and fecundity in marine invertebrates. The reserves deposited in the egg during oogenesis are assumed to be catabolized during embryogenesis prior to the formation of a functional larval digestive system. In fact, little is known about the metabolic fates of yolk proteins during embryogenesis (Yamashita & Indrasith 1988). Generalizations regarding the functional role of yolk in life histories are often unjustified because the organelles designated as "yolk bodies" may not play a nutritive role, and few experimental studies have confirmed the trophic role of yolk (Williams 1967). More importantly, it is not known if the various organelles described as yolk bodies are qualitatively and functionally similar in different species. Teleost (Wallace 1985, Sellman et al. 1988) and crustacean (Blades-Eckelbarger & Marcus 1992) biologists, for example, recently determined that some "yolk granules" are involved in the fertilization reaction and play no trophic role in development.

Echinoderms have played a central role

in discussions of the relationship between egg size and energy content (reviewed by Emler et al. 1987) but the results have often been confusing or contradictory. These collective investigations have shown that there is no simple relationship between egg size and energy content and that broad generalizations within and between taxa are not warranted. Recent studies of *Arbacia* development by Armant and co-workers (1986) demonstrated that there was no evidence of yolk platelet depletion during embryonic development to the pluteus stage (e.g., no decrease in concentration of yolk platelet protein was detected during development) although yolk platelet protein subsequently disappears during later larval development. The authors concluded that yolk might be used in the event the larva was unable to obtain food when feeding begins at the pluteus stage. In a related study of echinoid development, Scott & Lannarz (1989) reported limited proteolytic processing of yolk glycoproteins to lower molecular mass glycoproteins during the course of development but that the glycoproteins remained within the yolk platelet. In a comparative study of yolk proteins in the planktotrophic urchin *Heliocidaris tuberculata* and the direct developing species, *H. erythrogramma*, Scott and her co-workers (1990) found that eggs of the former species contained yolk protein within yolk bodies while the latter did not. Expecting to find a greater increase in yolk proteins in the larger, direct-developing eggs, they found much lower levels of glycoproteins. The authors considered these results consistent with the theory that yolk glycoproteins in sea urchins are not utilized in early development but rather during late larval and premetamorphic stages in planktotrophic species.

Strathmann & Vedder (1977) reported that organic matter per unit volume decreased with egg size in echinoderms with feeding larvae and predicted that such a trend may not be evident in eggs of larger

size. Turner & Lawrence (1979) confirmed the Strathmann & Vedder prediction and found no relationship between organic matter concentration and egg size with larger echinoderm eggs. McEdward & Chia (1991) recently reported no interspecific relationship between energy concentration (Joules/ul) and egg size for the pelagic lecithotrophs they examined. Due to compositional similarity of eggs of different sizes and developmental modes, some workers concluded that the significance of larger echinoderm eggs is not to accommodate the differences in the energetic demands of development, but rather to create a larger offspring (Lawrence et al. 1984). McClintock & Pearse (1986), in a study of three Antarctic echinoderms, found no direct correlation between egg size and energy content because no loss of energy was recorded during development from the egg to the juvenile. In some echinoderms, egg volume and energetic content varies within a single spawn of a single female (McEdward & Coulter 1987). In other species, egg size varies among individual females from the same population, and among individuals from different populations (Emlet et al. 1987). In the asteroid, *Solaster*, variation has been observed in egg size and organic content 1) among eggs from a single spawn, 2) among females from a single population, and 3) among populations (McEdward & Carson 1987). The authors point out that accurate estimates of egg volume cannot be obtained by simply measuring egg diameter for invertebrates because many eggs are spheroidal in shape. In the echinoid *Arbacia lixula*, egg size varied between different adult populations having different levels of available food with eggs and larvae significantly larger in the higher food population (George 1990). It is clear that the functional role of yolk deserves further study.

We will next assess the relationship between vitellogenic mechanisms and life history patterns. Specifically, is there a correla-

tion between the mechanism of vitellogenesis and the frequency of egg laying?

Vitellogenic Mechanisms and Breeding Frequency

Invertebrates differ significantly with respect to the timing of sexual maturity and the frequency of reproductive episodes. Species that breed only once are termed "semelparous" or "monotelic" (Cole 1954, Stearns 1976) (Fig. 4A). Among semelparous species, the age of reproduction may range from a few hours to several years. Those that breed several times are termed "iteroparous" or "polytelic" (Wynne-Edwards 1962, Clark & Olive 1973). Iteroparous species may be further subdivided to distinguish those that breed during a series of discrete episodes separated by periods of usually one year (annual iteroparity, e.g., many echinoderms) (Fig. 4B) and those breeding more or less continuously during an extended breeding season (continuous iteroparity), represented by many small-bodied polychaetes (Fig. 4C). Among iteroparous species that undergo repeated reproductive episodes, the period between successive breeding episodes can vary from hours to more than a year. Following the first reproductive episode, reproduction may then be repeated at various intervals ranging from daily to semiannually, annually, or biennially.

Ultrastructural studies of oocyte differentiation during the vitellogenic phase of oogenesis can be useful in determining the possible mechanism(s) of vitellogenesis utilized by a given species. Species utilizing heterosynthetic mechanisms often produce eggs rapidly and have short intervals between reproductive episodes while those utilizing autotrophic mechanisms generally demonstrate slow rates of egg production and have relatively long periods between reproductive episodes.

The level of endocytotic activity in grow-

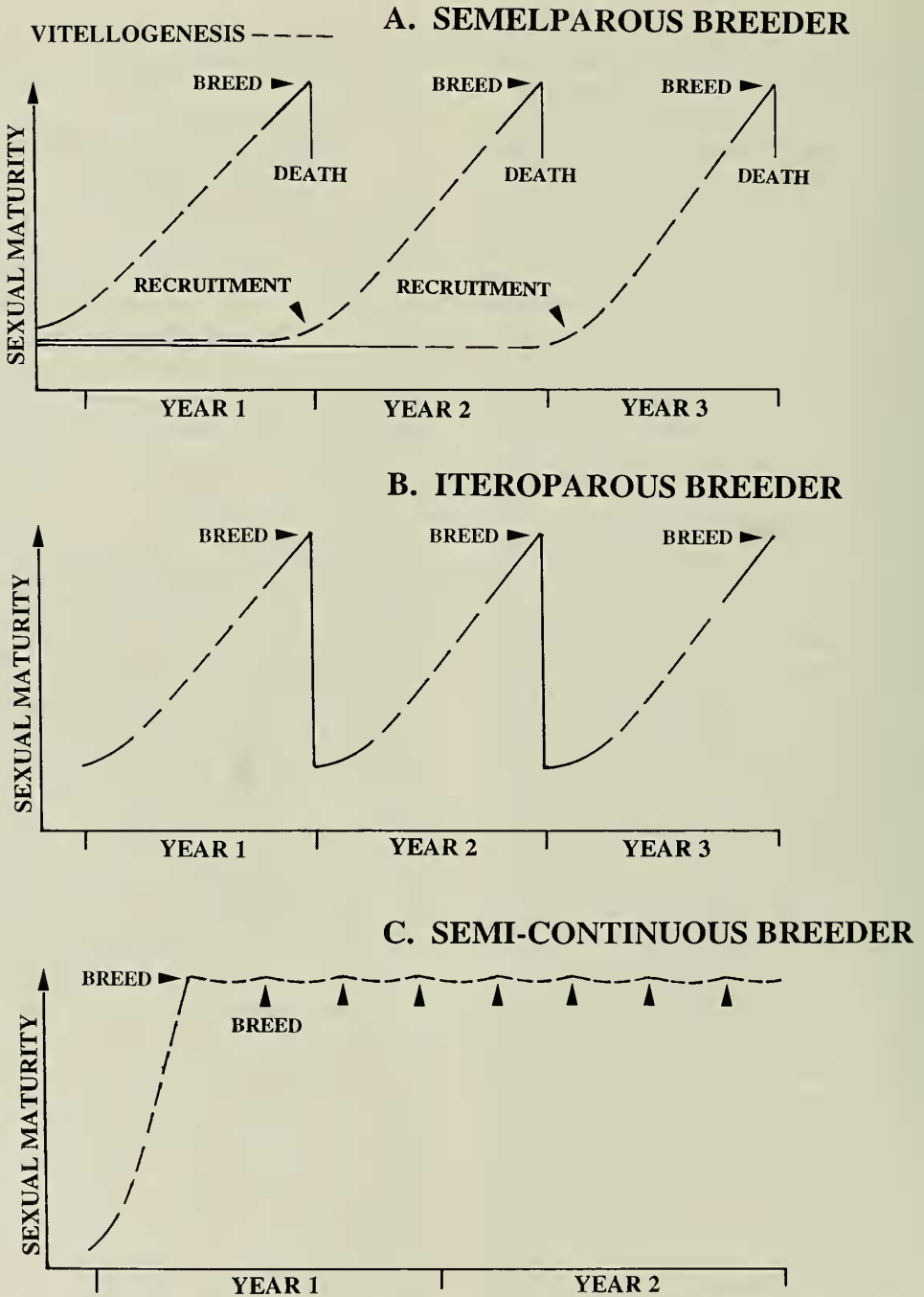


Fig. 4. Metazoan breeding patterns. A) semelparous breeder; B) iteroparous breeder; C) semi-continuous breeder.

ing oocytes is often positively correlated with the rate of oocyte growth. Semelparous and annual iteroparous species generally show low levels of endocytotic activity during vitellogenesis because there is no premium on rapid yolk precursor incorporation and yolk production. For example, endocytotic activity is minimal in most iteroparous echinoderms based on ultrastructural studies of asteroids, echinoids, crinoids, ophiuroids, and holothuroids (see review of Eckelbarger & Young 1992). However, the lack of significant endocytotic activity in growing oocytes does not suggest that exogenous precursors are not being incorporated but rather that they are being incorporated at a slow rate. The oocytes of the asteroid *Asterias rubens* are known to incorporate high molecular weight exogenous molecules despite the absence of ultrastructural documentation of endocytotic activity (Beijnick et al. 1984). Low endocytotic activity in growing oocytes may merely indicate a rate of precursor incorporation that is not easily detectable by ultrastructural methods. Oogenesis extends for a period of more than a year in the semelparous nereid polychaete *Nereis virens* (Brafield & Chapman 1967), and 7–8 mo in *N. grubei* (Schroeder 1968). The oocytes of both species show minimal endocytotic activity even though a female-specific yolk protein is known to be produced by coelomocytes and incorporated slowly over the long growth period (Fischer & Dhainaut 1985). Likewise, other semelparous nereids such as *Nereis diversicolor*, *N. pelagica*, *Perinereis cultrifera*, and *Platynereis dumerilii* have long periods of vitellogenesis and have little or no detectable endocytotic activity in the oocytes (reviewed in Fischer & Rabien 1985). Other polychaetes with slowly growing oocytes show a similar pattern of low endocytotic activity during vitellogenesis (Eckelbarger 1983, 1986). In contrast, oogenesis occurs in less than three months in the nereid *Neanthes arenaceodentata* (Davis 1969) and ultrastructural studies of their faster devel-

oping oocytes have shown high levels of endocytosis during vitellogenesis. Other polychaetes such as *Phragmatopoma lapedosa*, *Streblospio benedicti*, and *Polydora ligni* undergo vitellogenesis in only a few days and show high levels of endocytotic activity during this period (Eckelbarger 1979, 1980, 1983, 1986). Similarly, oocytes of the semaeostome jellyfish, *Aurelia aurita*, an iteroparous neritic species that undergoes rapid egg production, show intense endocytotic activity during vitellogenesis (Eckelbarger & Larson 1988). In insects, including most of the primitive Apterygota, vitellogenesis is a heterosynthetic process in which the fat body produces yolk protein precursors which are secreted into the hemolymph, and rapidly sequestered by the developing oocytes through a receptor-mediated process (Hagedorn & Kunkel 1979, Raikhel & Dhadialla 1992).

Ovarian nurse cells are frequently associated with rapidly developing oocytes, notably in the insects. Vitellogenesis occurs in only 25 h in the mosquito (Roth & Porter 1964) and about 18 h in the fruit fly, *Drosophila* (Brownes 1982), species having the more complex meroistic ovary containing nurse cell complexes. In contrast, in the more primitive panoistic insect ovary lacking nurse cells, vitellogenesis is relatively long, for instance, 3–6 mo in the cricket (in Davidson 1986). Ovarian nurse cells are also responsible for rapid egg growth in ctenophores, rotifers, annelids, and crustaceans (Davidson 1986). In the Ctenophora, the majority of biosynthetic activity during oogenesis appears to be performed by the large population of nurse cells that establish a syncytium with the oocyte (Pianka 1974). Yolk bodies are formed in the ooplasm by the fusion of pre-yolk bodies originating from the nurse cells. Vitellogenesis in ctenophores is believed to occur in only about two days in *Beroe gracilis* and *Pleurobrachia pileus* (Greve 1970). In the rotifer *Asplanchna* there is a 100-fold increase in oocyte volume within 4–6 h resulting from the

abrupt transfer of cytoplasmic materials to the oocyte from the syncytial nurse cells of the vitellarium (Bentfield 1971). Accelerated egg production occurs in the small-bodied polychaete, *Ophryotrocha puerilis* with the assistance of a single polyploid nurse cell (Ruthmann 1964). Among hydrozoans, nurse cells-assisted vitellogenesis reduces oogenesis to about four days in *Hydra carnea* (Honegger 1981) and less than eight days in *Tubularia crocea* (Mackie 1966).

Follicle cells are perhaps the most common accessory cell found in invertebrate ovaries and there are some examples in which their function(s) is directly correlated with rapid egg production. The opportunistic polychaete *Capitella jonesi* (Eckelbarger & Grassle 1982) undergoes frequent and rapid egg production with the aid of hypertrophic follicle cells that contribute to the production of yolk precursors during vitellogenesis. Follicle cells also have been shown to be the source of yolk precursors in the rapidly growing eggs of some bryozoans (Reed 1988, 1991). In chaetognaths, egg production can occur at daily intervals and may be facilitated by the endocytotic incorporation of precursors produced by follicle-like accessory cells (Shinn 1992).

The adaptive significance of semelparity and iteroparity has been debated extensively (see Grahame & Branch 1985); theory suggests that these respective life history patterns have evolved to attune the life style of the organism to its environment (Stearns 1976). Often overlooked is the fact that the duration of vitellogenesis is strikingly different between semelparous and iteroparous species. As reviewed above, different mechanisms of yolk synthesis have evolved in these organisms, including those that have endowed some species with the ability to rapidly accumulate yolk reserves. Rather than categorizing species as semelparous or iteroparous, it is more appropriate to view them on a continuum ranging from relatively fast egg producers characterized by heterosynthetic mechanisms designed to ac-

celerate yolk production, to relatively slow egg producers characterized by slower "mixed" mechanisms of yolk synthesis. As the period of vitellogenesis shortens (and the potential rate of egg production increases), the adoption of heterosynthetic mechanisms assisting the egg in yolk production increases. In the examples presented above, these mechanisms range from the direct transport of vitellogenin to the ovary through the blood, hemolymph or coelomic fluid, to trophic support from the biosynthetic activity of follicle cells and/or nurse cells (Fig. 1). The rapid incorporation of yolk precursors by receptor-mediated endocytosis is a common mechanism observed in species having rapidly growing oocytes. Fast egg producers and accompanying heterosynthetic mechanisms of yolk production are generally not found among annual spawners because selective pressures do not favor accelerated egg growth. In these species, "mixed" vitellogenic mechanisms have been adopted in which endocytotic incorporation of yolk precursors plays a lesser role during oocyte growth. Long-lived species have adopted mechanisms for slow egg production consistent with seasonal, continuous, or predictable food supplies and relatively stable environments that characterize shallow water populations at temperate latitudes. Unstable environments with unpredictable food supplies, on the other hand, favor fast egg producers (e.g., opportunistic species) and the accompanying evolution of accelerated mechanisms of yolk synthesis.

Energy Allocation and Oogenesis Among Slow vs. Fast Egg Producers

The manner in which organisms allocate energy among growth, maintenance and reproduction during each reproductive period is critical to their life history and will differ between species depending upon the vitellogenic mechanism employed. Reproduction and somatic growth are generally considered antagonistic and relatively long-lived

semelparous species (e.g., *Nereis virens*) often allocate some energy to both, whereas many species that breed semi-continuously (e.g., *Capitella* and *Streblospio*) appear to convert a large proportion of their energy directly into reproduction. In crustaceans, some species can sustain simultaneous gonadal maturation and somatic growth (including molting) while in others, growth is sacrificed at the expense of reproduction (Harrison 1990). Storage of energy reserves in the somatic tissues for later use during oogenesis is common in semelparous species. Many polychaetes, for example, store glycogen and lipid in the gut, peritoneum and coelomic cells for later transfer to the oocytes (reviewed in Eckelbarger 1983). Lipids are commonly stored by copepods from higher latitudes for later use in reproduction (Sargent & Henderson 1986). In nereid polychaetes and cephalopods, maternal muscle tissue is catabolized during vitellogenesis and is gradually incorporated from the coelomic fluid and the circulatory system, respectively, by the oocytes. Some species show an immediate reproductive response to environmental stress or an interruption of food supply. For example, in some fast-breeding polychaetes, the ovarian accessory cells are involved in the resorption of unspawned eggs presumably as a means of energy recycling and they also abruptly resorb oocytes in response to food deprivation or other environmental stresses which may create an energy deficit (Eckelbarger 1986). Regeneration also may impose energetic demands on the female by altering nutrient allocation during sexual reproduction. In some opportunistic polychaetes (e.g., *Capitella*), regenerating females show a delay in maturation and a marked decline in fecundity as compared to non-regenerating worms (Hill & Grassle 1981, Hill et al. 1982). In semelparous nereid polychaetes, regeneration is progressively inhibited as females approach reproductive maturity, indicating a shift in allocation of nutrient resources toward oogenesis (Hofmann 1976). Energy

allocation, therefore, differs significantly between fast and slow egg-producing species due to different physiological priorities (Fig. 5).

Reproductive Responses to Food Levels

Nutrition, vitellogenic mechanisms, and egg production are inextricably linked but species show significantly different responses to spatial and temporal variations in food quality and quantity in the marine environment. For example, some species show abrupt reproductive responses to food levels while others do not. These differences may be related to the type of vitellogenic mechanism employed during oogenesis. Reproductive responses to variations in food levels have been extensively documented in pelagic invertebrates (Checkley 1980) yet are poorly understood in benthic species (Levin & Creed 1986). Pelagic species show variable rates of food conversion into egg production and reproductive effort has been observed to be very sensitive to food level (Tester & Turner 1990, Razouls et al. 1991). The semaeostome scyphozoan, *Aurelia aurita*, maintains a high rate of egg production when fed but quickly resorbs its oocytes when deprived of food for as little as two days (Eckelbarger & Larson 1988 and unpubl.). Oogenesis is very short in this species and oocytes show high levels of endocytotic activity during vitellogenesis. In copepods, egg production for some species follows food ingestion within hours whereas, for others, the response may take days (Tester & Turner 1990). Vitellogenesis in *Calanus pacificus* is very rapid after feeding (Runge 1984) with labeled food appearing in oocytes in less than 8 h after food ingestion (Marshall & Orr 1956). Lower food levels slow the rate of yolk synthesis so that spawning intervals are longer and egg production rates are lower (Runge 1984). This species is adapted for rapidly converting nutrients to yolk and will have a short term advantage over species utilizing slower pathways for

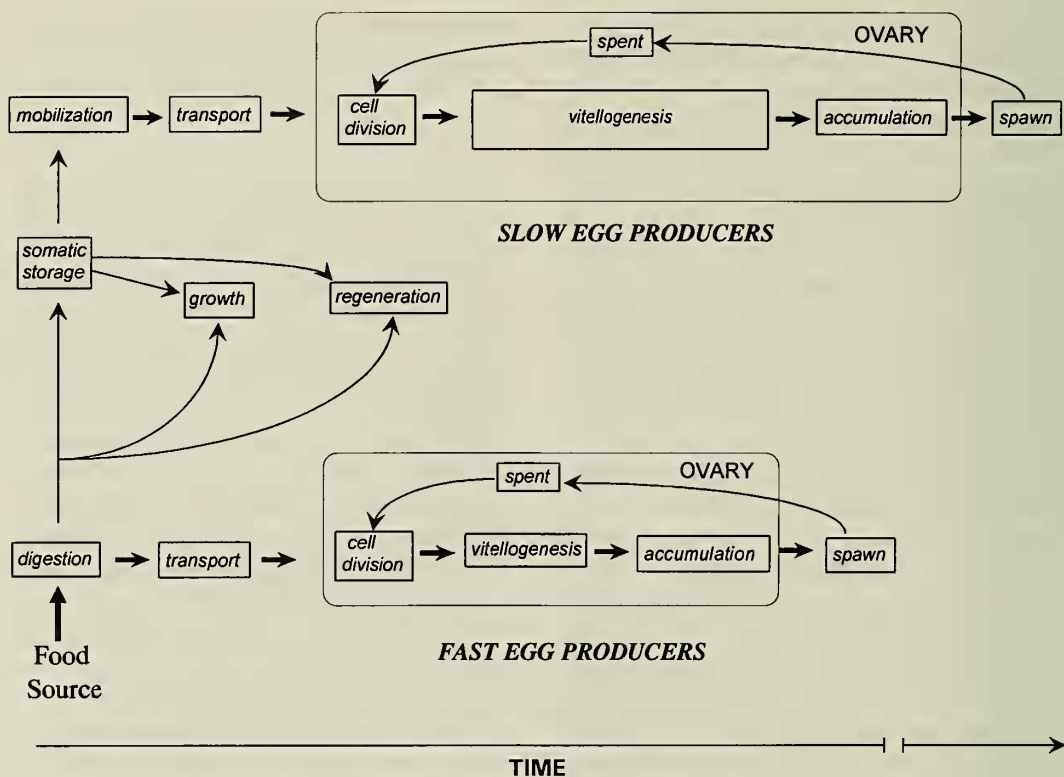


Fig. 5. Energy flow pathways from food source to spawned egg in slow and fast egg producers.

nutrient incorporation. Although the ultra-structural features of oogenesis have not been described in *C. pacificus*, they have been reported in *Labidocera aestiva*, another species that produces eggs rapidly. The oocytes of this species rapidly incorporate exogenous precursors endocytotically from the surrounding hemolymph (Blades-Eckelbarger & Youngbluth 1984). In contrast, the oceanic subantarctic copepod, *Neocalanus tonsa*, exhibits seasonal changes in feeding behavior, egg production response, and organic composition. Winter females dwelling in mesopelagic depths can release eggs in the absence of particulate food due to lipid reserves that allow recruitment to be decoupled from or out of phase with primary production in surface waters. Spring females, on the other hand, have limited lipid reserves and must obtain exogenous sources of nutrition for egg production. They

are, therefore, directly coupled to primary production for recruitment (Ohman 1987).

There are many examples of species that respond to feeding or starvation by abruptly switching egg production on or off. For example, while most sea anemones are annual breeders, store food reserves, have extended gametogenic periods, and show little immediate response to food levels (Jennison 1979), the small, estuarine anemone *Nematostella vectensis*, shows dramatic responses to food levels by producing eggs at 8-day intervals as long as feeding continues (Hand & Uhlinger 1992). The remarkable ability of some benthic species to translate increased food supply into accelerated egg production may underlie opportunistic dynamics in shallow water macrobenthos (Levin 1986). Populations of *Capitella* sp. I, for example, are extremely sensitive to changes in food supply and can adjust their

reproductive rates accordingly, an important determinant of opportunistic population dynamics (Marsh et al. 1989). The capitellid ovary is capable of rapidly producing yolk precursors in response to food intake with the aid of proteosynthetic follicle cells (Eckelbarger & Grassle 1982). However, even in capitellids, significant variation is observed in the way food is utilized in egg production (Eckelbarger 1986). Sibling species of *Capitella* occupy similar habitats and appear to have similar methods of vitellogenesis, but they show wide variation in egg volume, brood size, and the types of yolk materials deposited in the eggs (Eckelbarger & Grassle 1983): Despite their close genetic relationship and similar habitats, food is utilized differently by the ovary. In organic enrichment studies of *Streblospio benedicti*, a polychaete exhibiting both planktotrophic and lecithotrophic modes of larval development, females exhibiting lecithotrophy showed an increase in egg production while those with the planktotrophic mode showed no increase (Levin & Creed 1986). The eggs of *S. benedicti* contain two kinds of yolk bodies produced by separate autotrophic and heterotrophic pathways (Eckelbarger 1980) but the lecithotrophic egg contains a higher proportion of heterotrophically-derived yolk bodies (Eckelbarger 1986). The circulatory system of *S. benedicti* is capable of rapidly transporting yolk precursors to the ovary following feeding (Eckelbarger 1980). It has been suggested that this increase in egg production by females exhibiting lecithotrophic development could be due to a greater availability of heterotrophic yolk precursors derived from the enhanced food supply (Levin & Creed 1986).

The fact that reproductive responses to food varies (e.g., the existence of opportunistic and non-opportunistic species) suggests that there are complex interrelationships between trophic dynamics and reproductive biology that are poorly understood. However, recent comparative studies of gut morphology and kinematics of di-

gestive processing indicate that species operate under different digestive constraints related to their respective feeding ecologies (Penry & Jumars 1990). For example in polychaetes, the guts of carnivorous species differ morphologically and functionally from those of deposit feeding species (Penry & Jumars 1990) with carnivorous species having significantly less gut volume than deposit-feeding species. The diet of carnivorous species also contains greater proportions of high quality foods (higher protein, lower in ratios of carbon to nitrogen). Food quality rather than quantity is probably limiting for deposit feeders and the diets of deep-sea deposit feeders are believed to be, on average, of lower quality than nearshore and shelf deposit feeders (Penry & Jumars 1990). Food quality also influences digestion time. For example, diatoms and other labile foods are digested rapidly and absorbed efficiently while "seaweed detritus" requires long residence times. "Lignin" and other refractory organic matter is never appreciably absorbed (Lopez & Levington 1987). Many deposit feeding, opportunistic species such as those in *Capitella*, *Armandia*, *Tharyx*, *Cirratulus*, *Chaetozone*, *Paraprionospio*, *Levinsenia*, and *Streblospio* have simple guts that may be relatively inexpensive to construct and maintain but, due to short throughput times, may limit them to inhabiting areas of organic enrichment in order to exploit higher quality foods to support their high rate of reproduction (Penry & Jumars 1990).

Species apparently differ with respect to their trophic transfer efficiency (net production/food supplied) (Tenore 1983), so it cannot be assumed that similar foods will be energetically processed to support egg production in the same way in different species. In crustaceans, for example, optimal dietary balance and the efficiency of utilization of dietary carbohydrates, lipids, and proteins vary widely among species (Harrison 1990). In polychaetes, food quality and particularly nitrogen content appear to reg-

ulate growth and reproduction (Gremare et al. 1988). Juvenile growth has been shown to be especially sensitive to food quality with different growth responses being observed in relation to spring vs. summer detritus (Marsh et al. 1989). When considering population dynamics, interspecific dietary requirements and digestive constraints must be factored because they ultimately influence reproduction and growth. If species show different reproductive responses to nutrients, then nutrient levels in different habitats will present strong selective pressures favoring one species over another. For example, organic enrichment can have a dramatic effect on community structure and population biology of shallow-water organisms by decreasing diversity and increasing the resulting dominance by rapidly-reproducing, opportunistic species (Levin et al. 1993). Individual responses to elevated food quantity and/or quality may include increases in fecundity, early age at first reproduction, and modified egg composition (Levin & Creed 1986, Marsh et al. 1989, Qian & Chia 1991). Notable respondents to these enrichments include *Capitella* spp., *Polydora ligni* and *Streblospio benedicti*, which brood their young, have very high reproductive rates (Levin & Huggett 1990) and utilize heterosynthetic mechanisms of yolk acquisition (Eckelbarger 1983).

Vitellogenic Mechanisms and Habitat Instability

Some species have adopted mechanisms for rapid egg production that appear to be less related to food levels than to a response to inherent habitat instability. For example, life history studies of barnacles have demonstrated that species behave opportunistically to exploit changing conditions in rigorous, unpredictable environments by rapidly increasing yolk accumulation in response to food levels (Hines 1979). The intertidal, reef-building polychaete *Phragmatopoma lapidosa* is an opportunistic species with early age of first reproduction,

rapid and continuous egg production (Eckelbarger 1976) and unpredictable mortality due to storms and heavy wave action. Individuals are sexually mature soon after settling and are capable of spawning continuously. Oogenesis occurs in only two days and involves the transport of yolk precursors directly to the ovary via the circulatory system (Eckelbarger 1979) in a manner similar to that reported in the polychaete *Streblospio* (Eckelbarger 1980). Hydrothermal vent communities also represent ephemeral habitats whose age may be as short as 1–10 years (see Scheltema 1994). The fauna associated with these vents is largely unique and must mature and reproduce within a relatively short period of time so new active regions can be colonized. Recent studies of ovarian morphology and oogenesis in the vestimentiferan, *Riftia* sp. indicate that oocytes develop rapidly in close association with blood vessels (Gardiner et al. 1992) in a manner similar to some opportunistic polychaetes (e.g., *Streblospio*). Studies of vent-associated molluscs have shown that many species demonstrate life history traits that appear to be adaptive in this severe environment. Notable among these traits are rapid growth and continuous reproduction, which are probably related to a nutrient source that is relatively constant (Gustafson & Lutz 1994). Iteroparous molluscs that live longer and reproduce either intermittently or continuously throughout their reproductive life, tend to be found in more stable deep-sea environments (Scheltema 1994). Based on comparative studies of vitellogenesis, one would predict that unstable or unpredictable environments would select for species that mature early and reproduce rapidly using heterosynthetic mechanisms of egg production.

Vitellogenic Mechanisms, Food and Habitat Selection

If species convert food into egg production at different rates, one would expect that community structure would be influenced

by temporal variation in food levels. Community level responses to variable organic input are much better known for near-shore populations than for the deep sea (Jumars & Wheatcroft 1989). There has been a resurgent interest in benthic responses to temporal input of organic matter in the deep sea because of the growing realization that deep-sea organisms show a much higher frequency of seasonal reproduction than previously imagined, perhaps in response to environmental cues (Tyler et al. 1994). The relatively recent discovery of episodic inputs of significant organic food falls, plant material, and seasonal deposition of fresh phytodetritus on the deep-sea floor (see Scheltema 1994, for review) has stimulated great interest in determining whether benthic organisms show a reproductive response to these cues (Tyler et al. 1994). The deep-sea, wood-boring bivalve, *Xylophaga* sp., for example, shows an opportunistic life history by undergoing early sexual maturity, rapid egg reproduction, high population densities, and the ability to utilize a highly transient habitat (wood) similar to shallow water opportunistic species (Turner 1973). However, most deep-sea molluscs show no obvious coupling between seasonal periodicity of reproduction and primary productivity occurring at the ocean surface (Scheltema 1994). Scheltema (1994) suggests that seasonal differences in organic particulate flux may be largely irrelevant to many deep-sea molluscs except for filter feeders (e.g., Pectinidae), and possibly deposit-feeders that feed on the surface (e.g., protobranch bivalves). Omnivores, scavengers, and predators (i.e., majority of abyssal gastropods) may show little response to organic fluxes. Scheltema (1994) further suggests that other molluscs would only be secondarily affected. They include *Calypptogena* sp., a hydrothermal vent species harboring chemosynthetic bacteria, predatory or parasitic species affected directly by the relative abundance of their prey or host, and species that can derive much of their nutrition from dissolved organic materials in

the pore-water of deep-sea sediments (Southward & Southward 1982). In a study of species pairs of deep-sea organisms, one being a quasi-continuous breeder and the other a seasonal breeder, Tyler and colleagues (1994) studied the effects of seasonal phytodetrital pulses on reproduction. Their results indicated that all the quasi-continuous breeders conformed to the pattern predicted by showing no seasonal variation in their diet while in seasonal breeders, the pattern of reproduction did not vary with the supply of phytodetritus from the surface. Although seasonal reproduction has been widely reported among deep-sea invertebrates, control of these cycles is not necessarily related to these surface-derived fluxes (Tyler et al. 1994).

Do species show different reproductive responses to differing temporal patterns of organic input? Some regions of the deep sea receive a steady rain of organic material while others receive seasonal pulses resulting from surface plankton blooms (reviewed in Gage & Tyler 1991). In a recent study of energy metabolism by deep-sea benthic foraminifera, it was determined that at least two survival strategies have evolved in this group that reflect individual physiological responses to this variable input of food. Based on turnover times of ATP, some suspension feeding species respond to conditions in which they receive a steady rain of organic particles by showing a reduced ATP turnover rate, while some scavenging species respond rapidly to sudden, seasonal nutrient inputs with large seasonal ATP turnover rates (Linke 1992). This study supports the notion that adaptation to nutritional conditions rather than mass properties or physical conditions are the sole controls over foraminiferal distribution. The author suggested that organisms will evolve different survival strategies depending upon whether they live in environments receiving seasonal food input, such as epibenthic species living in temperate and Arctic latitudes, or if they are species exposed to little seasonality in food supply, such as in oligotrophic

regions of the ocean (Linke 1992). The downward vertical flux of surface phyto-detritus has been viewed as a potential controlling factor in gametogenic cycles and recruitment of seasonally breeding species (Tyler et al. 1994).

It remains an enigma that two or more sympatric species can have different reproductive patterns under the same environmental conditions (Tyler et al. 1994). However, it is relatively common to find congeners in similar habitats with completely different life histories even though the causes are often difficult to determine (Spight 1979). This situation implies that reproductive patterns are attuning the organism to something other than the habitat itself. When viewed from the perspective of vitellogenesis, these differences could be explained by interspecific differences in vitellogenic mechanisms and the manner of nutrient cycling during oogenesis. Since species have very different capacities to respond to organic enrichment it should not be surprising that even closely related species will show different responses to the same food levels. Animals of similar feeding types might exploit different organic components in different ways and at varying rates within the same habitat. Thus organic pulses of surface phytodetritus may be utilized in different ways by individual deposit feeders (or other animals) resulting in different life history responses. Studies of deep sea communities suggest that the strategy of sequestering labile food material by rapid assimilation and population growth is most effective for small organisms with rapid growth rates. This strategy is documented only for bacteria, microfaunal, and meiofaunal populations whereas the evidence for effectively sequestering pulses of raining organic matter for common deposit feeders of intermediate size (between echiurans and meiofauna or the macro-infauna) is very circumstantial (Jumars et al. 1990). Since organic windfalls to the deep sea bottom are

often unpredictable, it might explain why so many deep-sea populations contain individuals with only a few mature eggs at any given time (Rokop 1974, Gage & Tyler 1991) and the observation of a few juveniles present on average at any time (Grassle & Sanders 1973). Assuming that juvenile survival is highly variable, it would be useful for the adult to have many reproductive episodes with little energy and offspring invested in each (Jumars et al. 1990). As Jumars and his colleagues point out: "The relevant and unresolved issue for macrofaunal surface deposit feeders is whether these labile pulses are dominant, less important but still significant, or unimportant sources of the matter and energy shunted into production of this group of animals" (Jumars et al. 1990).

Echinoderms are among the most abundant macrofaunal organisms in the deep sea and their reproductive biology is better documented than for most invertebrate groups (Gage & Tyler 1991). Continuous reproduction in deep sea echinoderms is the most common pattern observed in the group but it involves the production of relatively few large eggs (Gage & Tyler 1991). Rapid and frequent egg production is rare in echinoderms, with the notable exception of the shallow water echinoid *Diadema* (Leviton 1988). Specialized heterosynthetic mechanisms for rapid yolk production have not been documented in the phylum and, thus far, vitellogenic mechanisms are highly conserved and of the "mixed" variety (Eckelbarger & Young 1992). Further, most echinoderms do not demonstrate abrupt reproductive responses to food levels. One would predict, therefore, that echinoderms would be well adapted to food conditions in the deep sea due to the prevalence of slow mechanisms of yolk synthesis characterizing the phylum. Seasonal cuing of organic pulses to reproduction are not likely to be strong because most species lack heterosynthetic pathways that would tightly couple nutrient input to egg production.

Table 1.—Some life history correlates of slow vs. fast egg producing species.

Fast egg producers	Intermediate	Slow egg producers
Heterosynthetic yolk production		"Mixed" (auto/heterosynthetic yolk production)
Relatively "r-selected"		Relatively "K-selected"
Small body size		Large body size
High food input		Low or seasonal food input
Low food reserve storage		High food reserve storage
Variable/unpredictable environments		Stable predictable environments
Short-lived		Long-lived
Low fecundity		High fecundity
Early sexual maturity		Late sexual maturity
High brood frequency		Low brood frequency

Conclusion

Efforts to comprehend the evolutionary forces that have shaped metazoan life history patterns must consider the role played by the ovary and the diverse mechanisms of yolk synthesis that have arisen through selection. Species have different capacities for converting food into egg production resulting in wide variation in the interval between reproductive episodes. These varying capacities are strongly influenced by the rate at which developing oocytes can synthesize yolk during oogenesis. Some species living in environments that are inherently unstable or experience sudden, large scale food inputs have evolved specialized mechanisms of yolk synthesis that enable them to respond to sudden nutrient input through rapid egg production. Other species, particularly long-lived iteroparous species, utilize slower methods of egg production and are adapted to stable environments that have seasonal or steady (predictable) inputs of nutrients. Therefore, vitellogenic mechanisms should play a central role in determining optimal species success in any given habitat based on differential reproductive responses to nutrients. In order to avoid simplistic life history models, the complex coupling between habitat, food, feeding strategies, digestive constraints, and vitellogenic mechanisms must be better understood in order to appreciate observed dif-

ferences in marine community structure. Table 1 lists some life history features that correlate with slow and fast egg-producing species.

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